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Phylogenetic Relationships among Genera of the Tetrabothriidae (Eucestoda)

Eric P. Hoberg

United States Department of Agriculture, eric.hoberg@ars.usda.gov

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PHYLOGENETIC RELATIONSHIPS AMONG GENERA OF THE TETRABOTHRIIDAE (EUCESTODA)*

Eric P. Hoberg

Department of Pathology and Microbiology, Atlantic Veterinary College, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island, Canada C1A 4P3

ABSTRACT: Cladistic analysis of the generic-level relationships within the family Tetrabothriidae was conducted. A single cladogram resulted from evaluation of 28 homologous transformation series representing 41 character states. The genus *Tetrabothrius* was recognized as plesiomorphic followed by *Chaetophallus* and *Trigonocotyle*. The latter was considered as the sister group for the remaining tetrabothriid genera of marine mammals. *Anophryocephalus, Strobilocephalus,* and *Priapocephalus* are among the most highly derived genera and are postulated as having close evolutionary affinities. Comparisons to previous explicit hypotheses for relationships among the genera indicated the present analysis was the most efficient phylogenetic statement (consistency index = 85.4%) for the 28 attributes evaluated. The recognition of *Tetrabothrius* as primitive and a natural grouping of *Anophryocephalus, Strobilocephalus,* and *Priapocephalus* in part confirmed results of previous studies of the Tetrabothriidae.

Tetrabothriidae Linton, 1891, constitutes a prominent group of cestodes among marine mammals and seabirds predominantly in pelagic ecosystems (Baer, 1954; Temirova and Skrjabin, 1978). Six genera are currently recognized: *Tetrabothrius* Rudolphi, 1819 (approximately 50 species among Procellariiformes, Sphenisciformes, Pelecaniformes, Charadriiformes, and Gaviiformes; and 8 species among Cetacea), *Chaetophallus* Nybelin, 1916 (2 species among Procellariiformes), *Strobilocephalus* Baer, 1932 (monotypic among Cetacea), *Priapocephalus* Nybelin, 1922 (3 species in Cetacea), *Trigonocotyle* Baer, 1932 (3 species in Cetacea), and *Anophryocephalus* Baylis, 1922 (3 species in Pinnipedia) (Temirova and Skrjabin, 1978; Schmidt, 1986). The tetrabothriids have been classified among the Pseudophyllidea (Nybelin, 1922), Cyclophyllidea (Fuhrmann, 1932; Wardle and McLeod, 1952; Schmidt, 1986; and others), as a suborder of the Tetraphyllidea (Spasskii, 1958; Temirova and Skrjabin, 1978) or in the separate order Tetrabothridea (Baer, 1954).

A tetraphyllidean relationship for the tetrabothriids had been considered previously by Baylis (1926) and later by Baer (1954). However, Baer's hypothesis suggested that tetrabothriids were a lineage of the Proteocephalidea that diverged as the sister group for all Tetraphyllidea. Alternative hypotheses for the origin of the tetrabothriids from tetraphyllideans were presented independently by Hoberg (1987a) and Galkin (1987) (see Spasskii, 1958; Temirova and Skrjabin, 1978). Studies of the structure and ontogeny of larval *Tetrabothrius* spp. supported a sister group relationship between the Tetrabothriidae and some derived tetraphyllideans (Hoberg, 1987a). Development of the metacestodes of *Tetrabothrius* and *Anophryocephalus* appears to share a homologous pattern with *Acanthobothrium* Beneden, 1849. Additionally, the holdfasts of many *Tetrabothrius* spp. (see Baer, 1954) appear most similar to those characteristics of *Ceratobothrium* Monticelli, 1892 (Oncobothriidae), or *Monorygma* Diesing, 1863, and *Dinobothrium* Beneden, 1889 (Phyllobothriidae) (Baylis, 1926; Williams, 1968; Hoberg, 1987a). These observations formed the basis for recognizing some of these tetraphyllideans as the putative sister group of the tetrabothriids.

Attempts to identify the original homeothermic hosts of the tetrabothriids (e.g., seabirds or marine mammals) have been equivocal. Baer (1932) suggested that pinnipeds were the primary hosts with subsequent colonization occurring independently among cetaceans and marine birds. Baer (1954) later recognized seabirds as primitive hosts, using host specificity as an indicator of relationship among genera and species, and considered that host-switching had occurred secondarily among marine mammals. Galkin (1987) attempted to refute the latter hypothesis for origin and diversification of the tetrabothriids, suggesting that marine mammals, particularly cetaceans, were the initial hosts. Hoberg (1987a) indicated that data were currently insufficient to corroborate any definite pattern of evolutionary

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relationships for hosts and parasites within the family, but he considered the probability that avian hosts were plesiomorphic.

Although the family has received attention in 2 monographs (Baer, 1954; Temirova and Skrjabin, 1978) the taxonomy and relationships among the genera and particularly for species referred to *Tetrabothrius* have remained confused. The validity of the 4 subgenera (*Tetrabothrius, Oriana, Neotetrabothrius,* and *Culmenamniculus*) suggested on morphological grounds by Baer (1954) and subsequently named by Murav'eva (1975) has not been well established (see Odening, 1982). Inadequate descriptions of the genital atrium and other characteristics in many species may not allow their reliable placement at the subgeneric level. Recent studies of *Tetrabothrius* spp. (Hoberg, 1987b) have indicated the necessity to reevaluate the status of many species because of incomplete documentation of intraspecific variation of major diagnostic characters (structure of genital atrium, length of male canal, number of testes) and because of the apparent lack of consistency in other morphological attributes. Among other genera, there has been considerable disagreement (Baer, 1932, 1954; Temirova and Skrjabin, 1978; Galkin, 1987) over the evolutionary affinities of *Anophryocephalus, Strobilocephalus,* and *Priapocephalus.*

As the basis for broader studies among the Tetrabothriidae, preliminary phylogenetic hypotheses, presented herein, were developed for generic-level relationships within the family. Completion of analyses among the genera (and later species) will promote the development of a natural classification for the group and provide a means of assessing earlier evaluations of evolutionary relationships (e.g., Baer, 1932, 1954).

MATERIALS AND METHODS

Relationships of 6 genera of Tetrabothriidae were analyzed using cladistics or phylogenetic systematics (Hennig, 1966; Wiley, 1981). The PAUP computer systematics program (Version 2.4), based on parsimony criteria, was used to construct phylogenetic hypotheses (Swofford, 1985). The small number of genera in the study group allowed analyses to be conducted with the ALLTREES option; trees were rooted with a designated ancestor and Farris optimization was employed (Swofford, 1985).

Specimens examined

Specimens of several *Tetrabothrius* spp. from avian hosts and representatives of all genera of tetrabothriids (except *Chaetophallus*) were examined. Material was borrowed from the U.S. National Museum (USNM), the British Museum of Natural History (BMNH) and from the collections of R. L. Rausch (RLR), and additional specimens are maintained in the author's collections (EPH). Specimens included: *Tetrabothrius shinni* Hoberg, 1987 (USNM 79657), *T. jagerskioldi* Nybelin, 1916, *T. cylindraceus* Rudolphi, 1819, *T. laccocephalus* Spätlich, 1909, and *T. erostris* Loennberg, 1896 (all EPH); *Trigonocotyle prudhoei* Markowski, 1955 (BMNH 1956.5.16.65–71, excluding material from *Lagenorhynchus australis* [Peale] and *Steno bredanensis* [Lesson]), *T. globicephalae* Baer, 1954 (BMNH 1956.5.16.63–64), *T. monticelli* (Linton, 1923) (USNM 8418 = *T. globicephalae*) and *Trigonocotyle* sp. (USNM 77368, 77679); *Strobilocephalus triangularis* (Diesing, 1850) (USNM 74662); *Priapocephalus* cf. *eschrichtii* Murav'eva and Treshchev, 1970 (RLR 31882); and *Anophryocephalus anophrys* Baylis, 1922 (BMNH 1922.5.3.1–6); *A. ochotensis* Deliamure and Krotov, 1955 (USNM 76200; RLR 7659), and *A. skrjabini* (Krotov and Deliamure, 1955) (USNM 75942, 75960, 76188, and 76178, all previously referred to *A. ochotensis*).

Character analysis

Homologous characters used in the analysis were derived primarily from the study of material representing tetrabothriids. Reference to detailed descriptions and redescriptions of tetrabothriids from marine mammals (Rees, 1956; Skrjabin and Murav'eva, 1972, 1978) and seabirds (Spätlich, 1909; Nybelin, 1916; Rawson, 1964; Burt, 1976, 1978; Andersen and Lysfjord, 1982), along with monographs on the Tetrabothriidae (Baer, 1932, 1954; Temirova and Skrjabin, 1978) and treatments of other cestodes (Linton, 1922; Fuhrmann, 1932; Wardle and McLeod, 1952; Williams, 1968; Schmidt, 1986) augmented the study. Polarization of character states was accomplished by outgroup comparison (Lundberg, 1972; Wiley, 1981). Primary outgroups were tetraphyllideans of the genera *Phyllobothrium* Beneden, 1849, *Dinobothrium, Monorygma,* and *Ceratobothrium.* These taxa were selected based on recognition of some derived Tetraphyllidea as the putative sister group for the Tetrabothriidae (see Spasskii, 1958; Hoberg, 1987a; Galkin, 1987).

Polarity of 3 characters (genital atrium [2]; male canal [3]; position of ovary [7, 8]) was reevaluated with reference to the functional outgroup (*Tetrabothrius*) following preliminary analyses (see Watrous and Wheeler, 1981). Four characters were split into independent transformation series to account for derivation of some character states (position of ovary [7, 8]; position of testes [10, 11]; shape of scolex [21, 22]; and structure of auricular appendages [27, 28]) (see Glen and Brooks, 1985; Hoberg, 1986). A summary of the 28 homologous series, representing 41 character states, is presented below and in a numerical matrix (Table I). Plesiomorphic states are coded as 0, apomorphic as 1, 2, or 3. In genera containing species exhibiting both primitive and derived states, specific characters were coded as plesiomorphic.

An integral part of the analysis included calculation of the consistency index (CI), a measure of the fit of specific characters to the hypothetical phylogeny (Farris, 1970). Values for CI were calculated for individual characters and for overall relationships within the family. Additionally, the CI was used as a basis of com-

parison of the present analysis with previous explicit phylogenies (Baer, 1932, 1954) via the TOPOLOGY function of PAUP (Swofford, 1985).

RESULTS

Characters

1) Genital pore (position). Two states: 0 = lateral; 1 = ventrolateral.

2) Genital atrium (structure). Among tetraphyllideans the genital atrium is unmodified, whereas, among all tetrabothriids, except *Priapocephalus,* it is complex. Coding of this character was accomplished by functional outgroup (*Tetrabothrius*) following preliminary analysis. Three states: 0 = with extensive muscular modification; 1 = dorsal component of atrium reduced, ventral aspect with deep muscular concavity; 2 = atrium weakly developed, with vestigial ventral concavity.

3) Male canal. A character unique to the Tetrabothriidae (Baer, 1954), except *Priapocephalus,* also coded by functional outgroup. Two states: 0 = present; 1 = absent.

4) Cirrus sac (shape). Two states: 0 = cylindrical; 1 = ovoid.

5) Uterine pore. Two states: 0 = multiple; 1 = single.

6) Uterus (extent). When completely gravid, the sacculate uterus may extend beyond the osmoregulatory canals. Two states: 0 = beyond canals; 1 = within canals.

7, 8) Ovary (position). Split into 2 transformation series (see Glen and Brooks, 1985; Hoberg, 1986) and coded with reference to the functional outgroup, the ovary may be in the anterior (0, 0), equatorial (0, 1), or posterior (1, 0) region of the proglottid. Character 7. Two states: 0 = anterior; 1 = posterior. Character 8. Two states: 0 = anterior; 1 = equatorial.

9) Testes (number). Two states: 0 = testes > 100; 1 = few testes.

10, 11) Testes (position). Split into separate transformation series, the testes may surround the ovary (0, 0), be postovarian (1, 0) or lateral to the ovary (0, 1). Character 10. Two states: 0 = surround; 1 = postovarian. Character 11. Two states: 0 = surround; 1 = lateral.

12) Testes (position). Two states: 0 = contained within osmoregulatory canals; 1 = extending beyond canals.

13) Testes (position). Two states: 0 = dorsal; 1 = dorsal and ventral fields.

14) Vitelline gland (form). Two states: 0 = follicular; 1 = compact.

TABLE I. Character matrix for the genera of Tetrabothriidae.

Genus	Character																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Tetraphyllidea*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetrabothrius Rudolphi, 1819	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaetophallus Nybelin, 1916	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Anophryocephalus Baylis, 1922	1	1	1	0	1	1	1	0	1	0	0	0	0	1	2	0	0	1	0	0	0	1	1	1	1	1	1	0
Strobilocephalus Baer, 1932	1	1	1	1	1	0	0	1	1	0	0	1	1	1	2	0	1	0	1	1	0	2	2	2	2	2	2	0
Priapocephalus Nybelin, 1922	1	2	2	0	0	0	0	1	0	0	1	1	1	0	2	1	1	1	1	1	0	2	3	3	3	2	3	0
Trigonocotyle Baer, 1932	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1

*Outgroups, including *Phyllobothrium* Beneden, 1849; *Dinobothrium* Beneden, 1889; *Monorygma* Diesing, 1863; and *Ceratobothrium* Monticelli, 1892.

TABLE II. Consistency indices of characters used in the analysis of the Tetrabothriidae.

Character number	Character	CI
1	Genital pore—position	1.0
2	Genital atrium—structure	1.0
3	Male canal	1.0
4	Cirrus sac—shape	0.50
5	Uterine pore	0.50
6	Uterus—extent	1.0
7	Ovary—position	0.50
8	Ovary—position	1.0
9	Testes—number	0.50
10	Testes—position	1.0
11	Testes—position	1.0
12	Testes—position	1.0
13	Testes—position	1.0
14	Vitelline gland—form	0.50
15	Neck—length	1.0
16	Genital ducts—position	1.0
17	Genital ducts—position	1.0
18	Osmoregulatory canals—dorsal	0.50
19	Scolex—osmoregulatory canals	1.0
20	Scolex—embedded	1.0
21	Scolex—shape	1.0
22	Scolex—shape	0.667
23	Bothridia—shape	1.0
24	Bothridia—depth	1.0
25	Bothridia—muscularization	1.0
26	Apical development	1.0
27	Auricles—structure	1.0
28	Auricles—structure	1.0

15) Neck (length). Two states: 0 = short; 1 = long.

16) Genital ducts (position). Two states: 0 = between osmoregulatory canals; 1 = ventral to canals.

17) Genital ducts (position). Two states: 0 = median; 1 = ventral.

18) Osmoregulatory system (dorsal canals). Two states: 0 = fully developed; 1 = atrophied.

19) Scolex (osmoregulatory canals). Two states: 0 = simple, tubular; 1 = subtegumental and reticulate.

20) Scolex (position in host). Two states: 0 = superficial contact with intestinal mucosa; 1 = embedded in mucosa.

21, 22) Scolex (shape). Split into separate transformation series, the scolex may be rectangular and flat (0, 0), rectangular and cuboidal (1, 0), round and flat (0, 1) or globular (0, 2). Character 21. Two states: 0 = rectangular and flat; 1 = rectangular and cuboidal. Character 22. Three states: 0 = rectangular and flat; 1 = round and flat; 2 = globular.

23) Bothridia (shape). Four states: 0 = rectangular; 1 = round; 2 = triangular; 3 = absent.

24) Bothridia (depth). Four states: 0 = shallow; 1 = intermediate; 2 = deep; 3 = absent.

25) Bothridia (muscularization). Four states: 0 = slight; 1 = moderate; 2 = great; 3 = absent.

26) Apical development (excluding auricular appendages). Three states: 0 = slight; 1 = moderate; 2 = great.

27, 28) Auricular structures. A complex character split into independent transformation series. In the genera *Tetrabothrius* and *Chaetophallus,* as in *Dinobothrium,* there is a single auricle fused to an anteromedial extension on each bothridium (0, 0) (see Spätlich, 1909; Linton, 1922; Baylis, 1926; Rees, 1956; Andersen and Lysfjord, 1982). In all species of *Anophryocephalus,* there are a pair of auricular structures, generally not fused, directed laterally and medially on the anterior margin of each bothridium (1, 0) (Baer, 1954; Murav'eva and Popov, 1976). In *Strobilocephalus,* there is a single auricle directed laterally from each bothridium (2, 0) (Baer, 1954). *Trigonocotyle* is characterized by 3 independent auricular appendages on the margins of the bothridia (0, 1) (Baer, 1932, 1954; Temirova and Skrjabin, 1978), whereas auricles are absent in *Priapocephalus* (3, 0). Character 27. Four states: as in *Tetrabothrius* (0); as in *Anophryocephalus* (1); as in *Strobilocephalus* (2); as in *Priapocephalus* (3). Character 28. Two states: similar to *Tetrabothrius* (0); as in *Trigonocotyle* (1).

Phylogeny of the Tetrabothriidae

A single cladogram for the 6 genera of Tetrabothriidae resulted from an analysis of 28 homologous series representing 41 character states (Fig. 1). This phylogenetic hypothesis was strongly supported with a CI of 85.4% (minimum length = 41; required changes = 48), indicating a good fit of these data to the cladogram. Consistency values for individual characters are presented in Table II. Homoplasy was postulated for parallel development in 1 character (ovoid cirrus sac in *Tetrabothrius* and *Strobilocephalus*) and evolutionary reversals of 6 additional attributes (uterine pore, position of ovary, number of testes, form of vitelline gland, dorsal osmoregulatory canals, and shape of scolex). These latter instances of homoplasy were largely associated with *Anophryocephalus, Strobilocephalus,* and *Priapocephalus.*

Monophyly for the Tetrabothriidae is strongly supported by a synapomorphy for the anteroventral position of the vitelline gland (a consistent character excluded from the present analysis). Additional characters including the dorsal uterine pore (5) and compact form of the vitelline

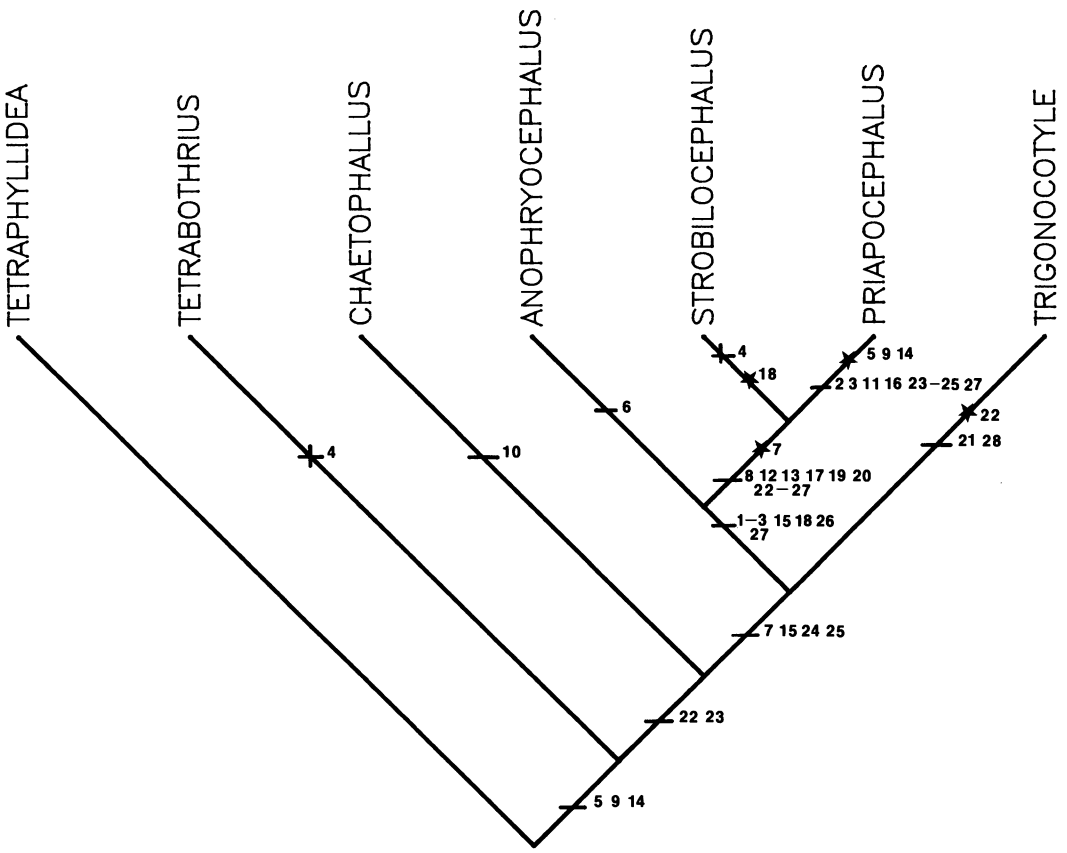

FIGURE 1. Cladogram for generic level relationships of the Tetrabothriidae. Apomorphic characters have been mapped on and designated by slashes; postulated evolutionary reversals and parallel development are indicated by stars and crosses, respectively. This hypothesis has a CI = 85.4% representing a minimum of 41 steps and 48 postulated changes.

gland (14) are constant within the group but have postulated evolutionary reversals associated with *Priapocephalus*.

The genera *Tetrabothrius* and *Chaetophallus* are postulated as relatively plesiomorphic with respect to *Anophryocephalus, Strobilocephalus,* and *Priapocephalus* (Fig. 1). The inclusive grouping of these latter genera results from the ventrolateral position of the genital pore (1), relatively long neck (15), and an atrophied dorsal osmoregulatory system (18). A sister group relationship for *Strobilocephalus* and *Priapocephalus* is based on 7 synapomorphies, particularly the extent of the testes beyond the osmoregulatory canals (12), ventral aspect of the genital ducts (17), and the reticulate structure of the osmoregulatory canals in the scolex (19).

Additional foundation for the derived relationship of *Priapocephalus* resulted from a subsidiary analysis in which all characters of the scolex and genital atrium (19–28; 2, 3) were deleted. Three cladograms of equal length (CI = 77.8%) were found. All differed slightly with respect to the topology of *Tetrabothrius, Chaetophallus,* and *Trigonocotyle* but not in the grouping or placement of the *Anophryocephalus–Priapocephalus* clade. This corroborates the character transformation series for the scolex and supports the sister group association of *Strobilocephalus* and *Priapocephalus*.

DISCUSSION

Character evolution

Analyses presented herein provide a foundation for postulating several trends in character evolution among the Tetrabothriidae. A suite of characters associated with the scolex has been influenced by hypertrophy of the apical region with concomitant reduction in the complexity and eventual loss of the auricles (as exemplified by *Priapocephalus*). A parallel situation is apparent in the simplification of the structurally

intricate genital atrium, which is most strongly developed among species of *Tetrabothrius*. Although these characters are of considerable diagnostic importance, their exclusion from the analysis does not substantially alter the topology of the cladogram (Fig. 1). Thus, robust support for this phylogenetic hypothesis is indicated and an *Anophryocephalus–Priapocephalus* clade appears to have a firm empirical basis.

Attributes of the scolex have figured prominently in attempts at explicit phylogenetic reconstruction for the tetrabothriids (Baer, 1932, 1954) or in discussions of generic evolution within the family (Baylis, 1926; Temirova and Skrjabin, 1978; Galkin, 1987; Hoberg, 1987a). Structural similarities of the scolex in *Tetrabothrius* spp. (4 auriculate bothridia) and some tetraphyllideans had been recognized previously (Baylis, 1926; Baer, 1954; Temirova and Skrjabin, 1978); however, the extent to which these attributes represented homologies was disputed (see Andersen and Lysfjord, 1982). Hoberg (1987a) provided independent ontogenetic data for *Tetrabothrius* that for the first time firmly corroborated hypotheses for scolex homology among tetrabothriids and tetraphyllideans. The presence of homologous auriculate appendages in *Tetrabothrius, Trigonocotyle,* and all species of *Anophryocephalus,* as reported herein and confirmed for *Strobilocephalus triangularis* (see Baer, 1954), establishes a basis for monophyly of these tetrabothriids.

In contrast to "typical tetrabothriids," *Priapocephalus* was characterized by an absence of auricular structures or vestigial bothridia (Baer, 1954; Temirova and Skrjabin, 1978). The amorphous, globular scolex characteristic of this genus, in conjunction with a number of plesiomorphic attributes (multiple uterine pores, follicular vitelline gland, elongate cirrus sac and apparent lack of a complex genital atrium) has contributed to the controversy about generic affinities of these cetacean parasites (Baer, 1932, 1954; Temirova and Skrjabin, 1978; Galkin, 1987). Baer (1932) considered *Priapocephalus* to be highly derived and close to *Strobilocephalus,* but he later (1954) suggested independent origins for both genera from advanced *Tetrabothrius* spp. among cetaceans. Temirova and Skrjabin (1978) considered *Priapocephalus* and *Tetrabothrius* as sister groups sharing a common ancestor (prototetrabothriid with tetraphyllidean affinities) while also suggesting that among representatives of the former, the scolex was highly modified.

Following detailed study of scoleces from immature specimens of *Priapocephalus,* Temirova and Skrjabin (1978) concluded that the globular holdfast actually represented a "pseudoscolex" that was derived secondarily from the anterior proglottids during early development in the definitive host (see Baer, 1954). Their contention was based on the structure of the parenchyma, presence of longitudinal musculature, and osmoregulatory canals. Thus, it was considered that the "true scolex" was lost during the initial stages of development and that the pseudoscolex was not structurally or ontogenetically homologous to holdfasts characteristic of other tetrabothriids. There was also a suggestion of paedomorphosis (postdisplacement; see Fink, 1982) in the ontogeny of the pseudoscolex as development was thought to be preceded by penetration of the intestinal mucosa of the definitive host by metacestodes.

Observations of *Priapocephalus* and *Strobilocephalus* during the present study appear to refute contentions by Baer (1954) and Temirova and Skrjabin (1978) concerning structure of the scolex. In both genera, there is a globular holdfast with extensive development of longitudinal musculature. Additionally, the osmoregulatory canals comprise a highly reticulate anastomosing system of tubules that are subtegumental in location. These attributes, in addition to other recognized synapomorphies linking *Strobilocephalus* and *Priapocephalus* (Fig. 1), support the placement of the latter genus and structural homology of the holdfast. However, the potential for paedomorphic development of the scolex in *Priapocephalus* is of considerable interest. Such a pattern would parallel that known (Hoberg, 1987a) for *Tetrabothrius* and *Anophryocephalus,* suggesting a degree of uniformity in morphogenesis of the adult holdfast within the family Tetrabothriidae. This heterochronic sequence in ontogeny of the scolex is thought to be unique among the Eucestoda (Hoberg, 1987a).

Comparison of phylogenies

Baer (1932, 1954) presented the only explicit phylogenies for genera of the Tetrabothriidae, whereas Rees (1956), Temirova and Skrjabin (1978), Galkin (1987), and Hoberg (1987a) discussed some potential relationships among the genera. The evolutionary trees developed by Baer were redrawn (Figs. 2, 3) to allow direct comparison with the present phylogeny via the TOPOLOGY function of PAUP (Swofford, 1985).

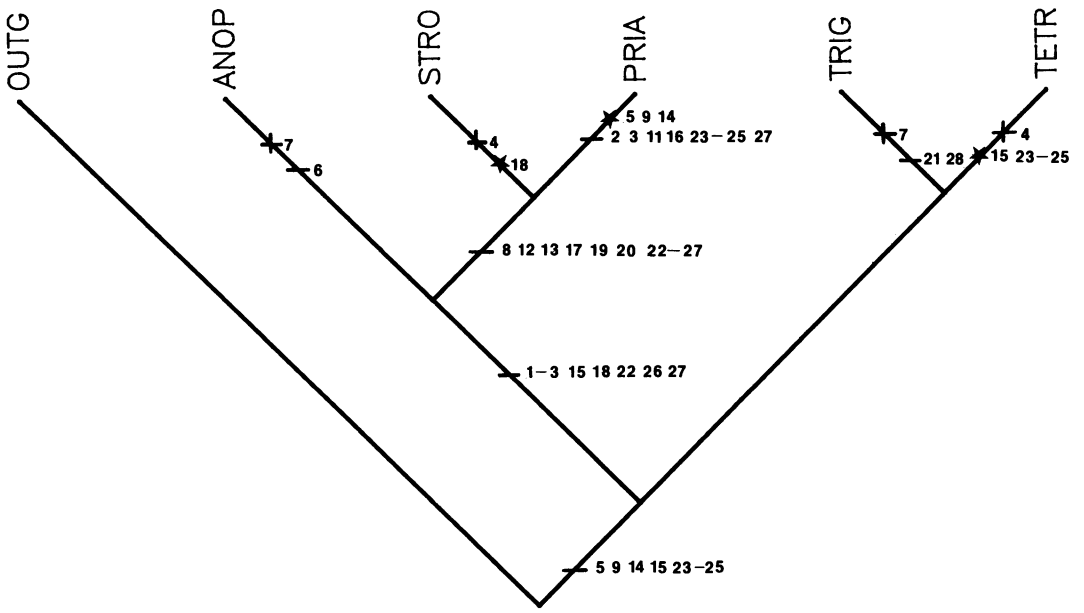

FIGURE 2. Cladogram prepared from phylogeny by Baer (1932) with character evolution evaluated by TOPOLOGY function. Characters are those in Figure 1; CI = 80% representing a minimum of 40 steps and 50 postulated changes (*Chaetophallus* deleted from analysis). Branch labels: OUTG, outgroup; ANOP, *Anophryocephalus*; STRO, *Strobilocephalus*; PRIA, *Priapocephalus*; TRIG, *Trigonocotyle*; TETR, *Tetrabothrius*.

Characters were mapped onto these alternative trees and optimized by Farris optimization (Farris, 1970) to allow a determination of the efficiency of the competing hypotheses (see Brooks et al., 1985a).

Baer (1932) recognized 2 lines of evolution from *Anophryocephalus*. Based on the assumption that auricular appendages were absent in *Anophryocephalus*, progressive development of the apical region led to the derivation of *Strobilocephalus* and *Priapocephalus* (Fig. 2). In contrast, modification of the apical region with development of auricular appendages occurred in *Trigonocotyle* and *Tetrabothrius* (here including *Chaetophallus* with *Tetrabothrius*). Although the grouping of *Anophryocephalus, Strobilocephalus* and *Priapocephalus* is supported, Baer's (1932) hypothesis is less efficient (CI = 80%, length = 50 steps; versus 87% for the present cladogram with *Chaetophallus* deleted). Evolutionary reversals are postulated for 8 characters (5, 9, 14, 15, 18, 23, 24, 25) and parallel development for 2 attributes (4,7).

The more detailed phylogeny postulated by Baer (1954) was considerably less parsimonious (CI = 57.7%; length = 71 steps) with parallel derivation (characters 4, 7, 8, 12, 13, 17, 18, 19, 20, 22, 26) and evolutionary reversals (1, 2, 3, 5, 9, 14, 15, 22, 23, 24, 25, 26, 27) of 11 and 13 characters, respectively. Figure 3 was drawn to recognize Baer's (1954) contention that avian tetrabothriids were primitive and that 2 advanced lineages were apparent among genera in mammalian hosts. Consequently, *Chaetophallus*, with the "classical type scolex," represents species of *Tetrabothrius* that Baer (1954) considered to be among the most primitive of those occurring among avian hosts (Procellariiformes). Extensive radiation of *Tetrabothrius* spp. occurred among seabirds but was apparently accompanied by minimal morphological diversification of the scolex (Baer, 1954). In contrast, species of *Tetrabothrius* among marine mammals were thought to be derived from those among seabirds with subsequent evolution involving trends in the reduction of the bothridia and atrophy of the apical region (Baer, 1954; Rees, 1956). Thus, *Trigonocotyle* was considered as originating independently from this latter group of *Tetrabothrius* spp. with continued alteration of the auricles and atrophy of the apical zone. However, hypertrophy of the apical region was postulated for *Anophryocephalus, Strobilocephalus* and *Priapocephalus*, with the latter also being independently derived from *Tetrabothrius* spp. among cetaceans. These hypotheses for independent derivation, adaptation, and convergence account for the increased length of the tree, and 7 of 11 cases

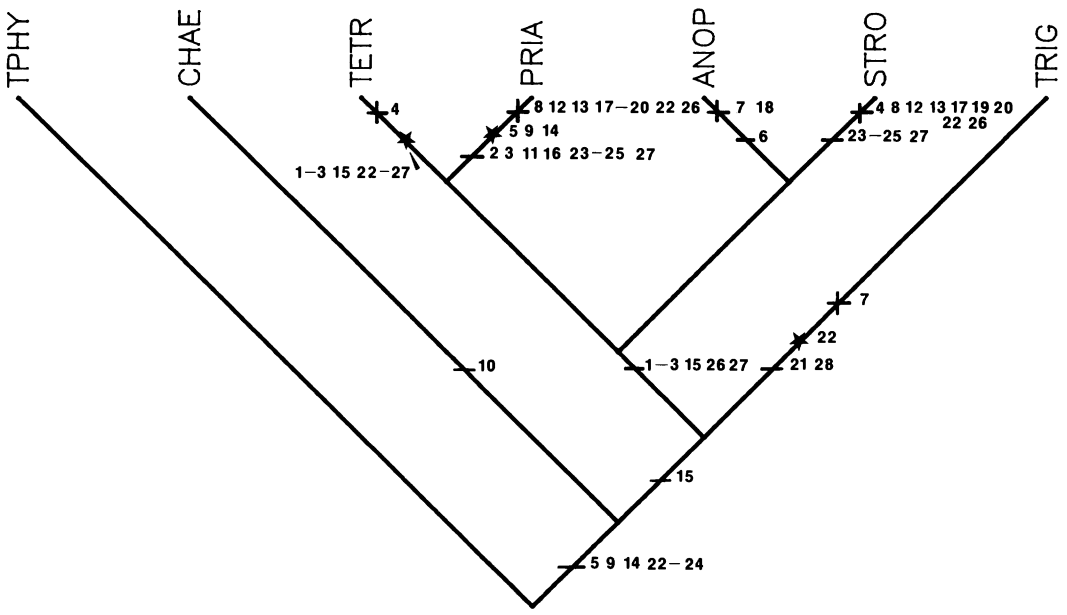

FIGURE 3. Cladogram prepared from phylogeny by Baer (1954), with character evolution evaluated by TOPOLOGY function. Characters are those in Figure 1; CI = 57.7% representing a minimum of 41 steps and 71 postulated changes. Branch labels as in Figure 2 except OUTG is replaced by TPHY, Tetraphyllidea.

of parallel evolution are postulated for *Strobilocephalus* and *Priapocephalus*.

Temirova and Skrjabin (1978) suggested that *Tetrabothrius* and *Priapocephalus* shared a common ancestor directly related to tetraphyllideans. Relationships of other genera were unresolved although they suggested that *Anophryocephalus* and *Trigonocotyle* were phylogenetically younger and derived from *Tetrabothrius*. *Strobilocephalus* was thought to be without definite association, an opinion refuted in the present study by synapomorphies associated with the genital atrium in the former genus and *Anophryocephalus*.

Galkin (1987) and Hoberg (1987a) considered *Tetrabothrius* as relatively primitive while suggesting a derived status for such genera as *Anophryocephalus* and *Priapocephalus*. Galkin (1987) in accordance with Baer (1932, 1954) and Rees (1956) suggested that *Anophryocephalus* represented the base of a lineage in which ensued progressive development of the apical region.

Conclusions

The present analysis constitutes a more efficient phylogenetic hypothesis for generic-level relationships within Tetrabothriidae than those provided in previous studies. Characters of the scolex and genital atrium have been the primary attributes considered in earlier evaluations (Baer, 1932, 1954; Rees, 1956; Temirova and Skrjabin, 1978). Although such were important in the current study, a suite of other homologous characters, not previously considered in evolutionary studies of the family, strongly supported the cladogram. In concordance with some previous studies, *Tetrabothrius* was postulated as relatively plesiomorphic (Baer, 1954; Rees, 1956; Temirova and Skrjabin, 1978; Galkin, 1987; Hoberg, 1987a) and the natural grouping of *Anophryocephalus, Strobilocephalus,* and *Priapocephalus* was reinforced (Baer, 1932; Hoberg, 1987a). Completion of phylogenetic analyses of genera and species of the Tetrabothriidae will provide for development of a natural classification for the group, an objective means of assessing previous phylogenetic hypotheses for relationships among species (e.g., Baer, 1954), and a basis of comparison to determine the degree of congruence between the phylogenetic histories of parasites and hosts as an indicator of parasite–host coevolution or colonization (see Brooks and Wiley, 1986; Brooks, 1988). The latter also may promote an evaluation of the role of parasite adaptive radiation in the evolution of this marine parasite fauna (see Brooks et al., 1985b; Hoberg, 1986, 1987a).

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